TAXONOMY, STRATIGRAPHY AND PALAEOBIOGEOGRAPHY OF PERMIANELLIDS (BRACHIOPODA)

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SHEN SHUZHONG & SHI, G. R., 1998:11:30. Taxonomy, stratigraphy and palaeobiogeography of permianellids (Brachiopoda). *Proceedings of the Royal Society of Victoria* 110(1/2): 267–279. ISSN 0035-9211.

Permianellids are characterised by bilobate valves, well-developed central platform, total lack of septal apparatus and umbonal attachment. Based on the present data, four genera, namely, *Dicystoconcha* Termier et al. 1974; *Permianella* He & Zhu 1979; *Litocothia* Grant 1976 and *Laterispina* Wang & Jin 1991 are recognised and their synonyms are listed. Chronostratigraphically they range from the Kungurian to the latest Changhsingian. Palaeogeographically, permianellids are extensively found in the Palaeotethys and the transitional zones between the Palaeotethyan and Boreal Realms, and between the Palaeotethyan and Gondwanan Realms.

PERMIANELLIDS are unusual not only in their shape and outline, but also in terms of their internal structure and living style, which has attracted much attention among brachiopodologists. The earliest record of permianellid brachiopods is the specimens figured as *Loczyella*? *parvula* Licharew by Licharew (1930: 436, text-figs 1, 2) and refigured by Licharew (1937: 132, pl. 13, figs 25–27) from the Upper Permian of North Caucasus, but they are permianellids (Jin Yugan, pers. comm.). Termier et al. (1974) described a permianellid, *Dicystoconcha lapparenti* Termier et al. 1974, as a species of lyttoniids based on a specimen from the Murgabian (*Neoschwagerina* Zone) strata in central Afghanistan. Since then, permianellids have been reported from: (1) South China (He & Zhu 1979; Liang 1982, 1990; Yang 1984; Mou & Liu 1989; Zhu 1990; Wang & Jin 1991; Shen et al. 1994, 1996); (2) Thailand (Grant 1976; Yanagida 1988); (3) Japan (Tazawa 1987, 1991, 1992; Shen & Tazawa 1997); (4) Primorye, Russia (Likharew & Kotljar 1978), North Caucasus (Licharew 1930, 1937), Transcaucasia (Shen & Shi 1997); and (5) Jilin and Inner Mongolia of Northeast China (Wang & Jin 1991).

The permianellids are generally characterised by bilobate shell, ovate or elongately ovate outline, concavo- and plano-convex profile, pseudopunctate shell, internal central platform and absence of septal apparatus. The classification and taxonomic nomenclature of permianellids are at present confusing, because of incomplete preservation of materials and differing interpretations among researchers. He & Zhu (1979), He et al. (1990) and Liang (1990) respectively upgraded the permianellids as a new Order Permianellida He & Zhu or Suborder Dipunctellidina Liang. Other authors have classified their permianellid specimens in the Lyttonioidea Waagen (Termier et al. 1974; Grant 1976; Wang & Jin 1991; Shen et al. 1994, 1996), Productoidea Gray (Liang 1982; Yang 1984), or Terebratulida Waagen (Mou & Liu 1989). Recently, with the further study of the shell fabric, internal structure, and palaeoecology of permianellids, it has been increasingly accepted that the permianellids belong to the Superfamily Lyttonioidea Waagen 1883 (Termier et al. 1974; Grant 1976; Wang & Jin 1991; Shen et al. 1994; Shen & Shi 1997). However, lower level classification within the Lyttonioidea remains uncertain. Our purpose is to clarify the external and internal features and synonyms of the permianellids and discuss their stratigraphical range and palaeogeographical distribution.

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA

Order PRODUCTIDA
Sarytcheva & Sokolskaja, 1959

Suborder STROPHALOSIIDINA Waagen, 1883

Superfamily LYTTONIOIDEA Waagen, 1883

Family PERMIANELLIDAE He & Zhu, 1979

Diagnosis. Bilobate lyttoniids with an anterior incision and an attachment ring on the posterior portion of the shell, concavo- or plano-convex in profile; irregular marginal brim or fence-shaped brim developed along the lateral sides or absent. Surface smooth except growth lines, spines absent. Ventral interior totally lacking internal septa, but usually with a central platform, a median septum or two lateral septa present on the central platform. Dorsal interior with longitudinal ridges along each lobe; brachial processes prominent. Shell fabric consists of external pseudopunctate layer and inner laminar layer.

External morphology. Permianellids are variable in size. Genera in the Family Permianellidae undergo progressive increase in size from the Kungurian to the Changhsingian although they had a relatively short stratigraphical range. The specimens of *Dicystoconcha lapparenti* Termier et al. from the Maan Member (Kungurian) of the Chihsia Formation are small (Yang 1984: 333). All others are relatively larger except the immature shell of *Litocothia cateora* Grant possibly from the Wordian which is only 7.0 mm in length and 11.5 mm in width (Grant 1976: 167). The largest species, *Laterispina parallela* Shen et al. from the Changhsingian of South China is 98.0 mm long (Shen et al. 1994: 480). Generally, their sizes, usually referring to their lengths, greatly increase stratigraphically and exceed their width in adults. But most species of permianellids attain a fairly large length with a relatively minor increase in width except the species *Lateríspina liaoi* Wang & Jin, in which the width evenly increases with its length (Fig. 1).

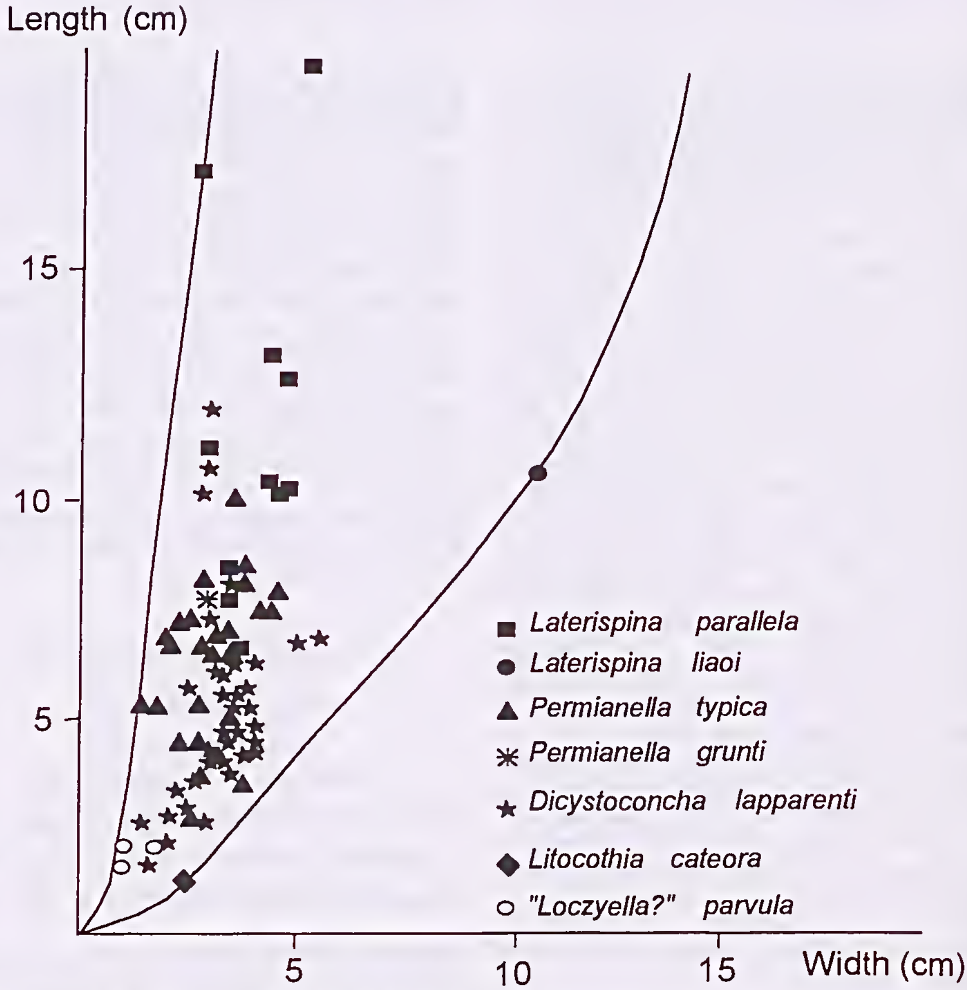

Fig. 1. Individual size distribution of reported permianellids.

In permianellids both valves are usually flat or strongly curved dorsally in lateral profile. The dorsal valve is normally slightly concave or nearly flat, but the ventral valve commonly strongly arched in transverse profile. Both valves consist of two lobes bisected by a shallow or deep incision at anterior commissure, forming the bilobate outline and emarginate anterior commissure. The lobes are always anteriorly directed, strongly elongated, and symmetrical or asymmetrical, producing various outlines: ovate, elongate ovate, lens-shaped, broadly triangular, narrowly triangular and band-shaped (Fig. 2).

The hinge line is recessed for reception of the dorsal valve, only seen in dorsal view, and very short, as characteristic of lyttoniids. The attachment ring on the posterior area is commonly very large, reflecting some cylindrical object, most likely crinoid stems, a feature also characteristic of many Lyttonioidea. The ventral sulcus of permianellids begins at the umbo, truncated by incision. The dorsal fold is usually flatly elevated. The types of lateral margins of the ventral valve are of generic importance in permianellids. *Dicystoconcha* Termier et al. and *Litocothia* Grant usually lack marginal brim around the lateral edge. However, *Permianella* He & Zhu has an irregular wing-shaped marginal brim around the lateral edge and *Laterispina* Wang & Jin has a complicated spine-like marginal brim. The surface of both valves is smooth except for some fine concentric growth lines. There are no spines or endospines in permianellids, which readily distinguishes them from common productids. The genus *Laterispina* Wang & Jin has a spine-like marginal brim along the lateral edge of the ventral valve, but these 'spines' are completely different from productid spines since they do not penetrate the shell and probably are rolled up by the marginal brim.

Internal morphology. On the internal face of the ventral valve of permianellids, there are two small

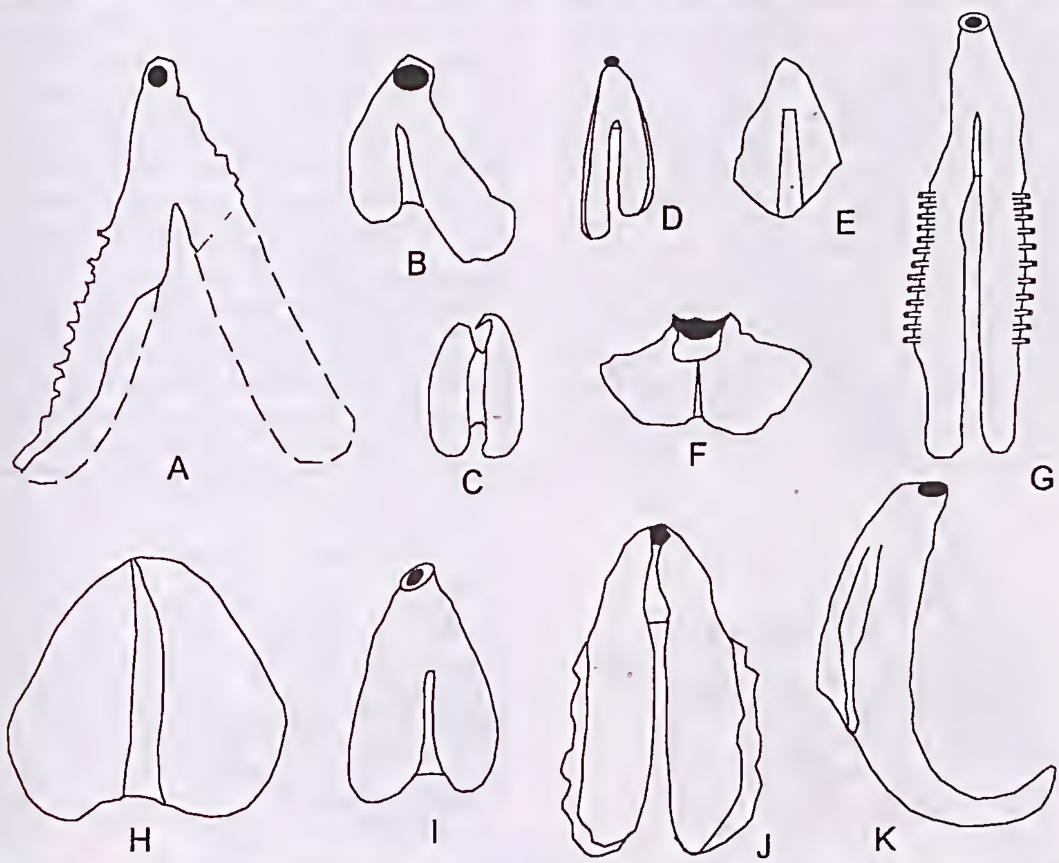

Fig. 2. Various outlines of permianellids. A, *Laterispina liaoi* Wang & Jin. B, C, H, I, K, *Dicystoconcha lapparenti* Termier et al. D, *Permianella grunti* Shen & Shi. E, '*Loczyella*?' *parvula* Licharew. F, *Litocothia cateora* Grant. G, *Laterispina parallela* Shen et al. J, *Permianella typica* He & Zhu.

recessed teeth (He & Zhu 1979: pl. 1, fig. 1b; Wang & Jin 1991: pl. 2, fig. 6). The central platform is characteristic of permianellids despite its variation among the genera. In the genus *Litocothia* Grant, the central platform is represented by a rounded-crest median ridge like some other lyttoniids. In other genera the central platform is usually hollow and trapezoid in transverse section, but becomes triangular posteriorly and filled by irregular inner septa in the youngest species *Laterispina parallela* (Shen et al. 1994: pl. 2, figs 1, 2, 8, 9). A median septum, commonly greatly enlarged and thickened posteriorly, is usually distorted and hence easily mistaken as a lateral septum. In some species two lateral septa are well developed on the central platform. Septa are short or long. A muscle scar is probably located on the central platform, perhaps symmetrical, but inconspicuous (Fig. 3A).

In the dorsal valve the sockets are roundly triangular, defined by inner socket ridges (Wang & Jin 1991: 487, text-fig. 3E). Cardinal processes are formed from two convergent inner socket ridges, spherical and slightly higher than the hinge line (Wang & Jin 1991: 487, text-fig. 3F). Brachiophore processes are unknown for *Dicystoconcha* and *Litocothia*, but well developed in the younger genus *Laterispina* Wang & Jin (Shen et al. 1994: pl. 2, figs 4, 6). These two processes, which are very similar to crura in some rhynchonellids, are rod-like, strongly projecting into the ventral cavity. Two low longitudinal brachial ridges, beginning from the floor of brachiophores, extend anteriorly for more than two thirds of the shell length. The inner edge at the lateral margin is commonly thickened and has a long marginal ridge well articulated with the corresponding groove of the ventral valve. The inner surface of both valves is smooth (Fig. 3B).

The shell fabric in the Permianellidae consists of an external pseudopunctate layer, often relatively thick and an internal lamellar layer as in the common lyttoniids. Shell fibres commonly curve outwards along pseudopuncta. The pseudopunctate layer of the dorsal valve is commonly thickened posteriorly. The attachment ring has a pseudopunctate layer only (Shen et al. 1994; Shen & Tazawa 1997).

Lithology. The strata yielding permianellid fossils are most commonly composed of mudstone, limestone or argillaceous limestone. Permianellids are also found in siliceous limestones, and tuffaceous sandstones. Associated organisms are usually various, but normally including benthic organisms such as crinoids, corals, fusulinids and bryozoans, indicating a normal shallow marine environment.

Life habits. All permianellids have an attachment ring on the posterior edge of the ventral valve, suggesting that they were attached at the beak and the shells probably rotated around their attached objects, changing their orientation in response to the changing currents. However, serial sections (Shen et al. 1994: 478, fig. 1.1–1.3) seem to eliminate the possibility that permianellids could slide down and up during their living time. The attachment ring is usually incompletely circular and either open-ended or occasionally joined to form an enclosed circle at posterior end. The circular or semi-circular attachment structure suggests that permianellids were attached to some cylindrical objects and belong to the higher epizoan suspension feeders (Wang & Jin 1991). Well-preserved specimens usually show that the attached objects are crinoid stems. Several individuals attached to a crinoid stem were also reported (Mou & Liu 1989: pl. 1, figs 6, 7; Wang & Jin 1991: pl. 1, fig. 8), indicating their population life. The

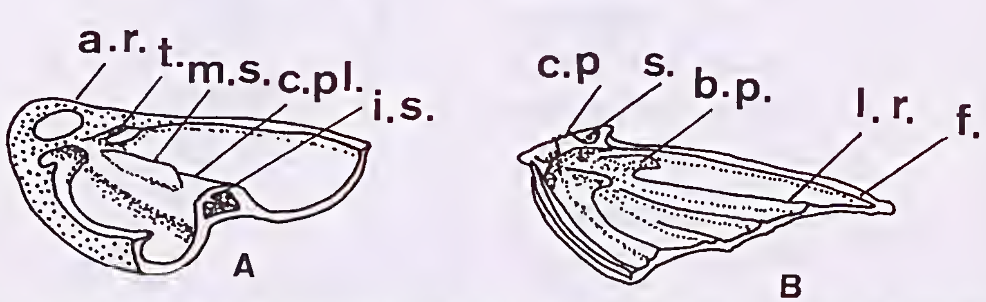

Fig. 3. Internal details of permianellids (after Wang & Jin 1991, revised by Shen et al. 1994). A, ventral valve; a.r., attachment ring; t., teeth; m.s., median septum; c.pl., central platform; i.s., internal septum. B, dorsal valve; c.p., cardinal process; s., socket; b.p., brachiophore process; l.r., longitudinal ridge; f., flange.

habits of living benthos attached to crinoids have been well documented among dead brachiopods, especially among lyttoniids (Wanner 1935: 243, 248, pls 6–9; Stehli 1954: pl. 19, fig. 1; Wright 1968: 263; Cooper & Grant 1974: pl. 127, figs 19–21, pl. 164, figs 9–11; Grant 1963: 136, 1976: 166, pl. 30, figs 19–23).

In view of permianellids bilobate shell and usually elongate outline, it can be interpreted that the permianellids may have hung their shells obliquely or vertically on the host above the substrate (Fig. 4). Their lobes strongly project anteriorly, indicating free growth expansion anteriorly. The freely suspended living state suggests that they do not need very strong muscles to open their valves. Individual permianellid specimens, obliquely or horizontally attached on the host, are usually curved dorsally. The lophophore of permianellids are simply schizolophous. The complicated marginal brims of the ventral valve suggest that at least part of their mantle was exposed.

Remarks. It is generally accepted that permianellids belong to the Superfamily Lyttonioidea Waagen in view of their distinctive hinge area, bilobate outline, pseudopunctate shell fabric and the total lack of spines or endospines. However, the position of permianellids within the Lyttonioidea has been a matter of considerable difference. Wang & Jin (1991) and Shen et al. (1994) considered that the permianellids should belong to an independent family, whereas Brunton et al. (1995) placed them in the Family Lyttoniidae Waagen, as a subfamily (Permianellinae He & Zhu). The Lyttoniidae brachiopods are characterised by their typically lobate dorsal valve and relatively complete ventral valve equipped with a complementary septal apparatus. No teeth are found in the ventral valve except for a pair of striated, convex surfaces occurring in the apical region. Unlike the Lyttoniidae, permianellids are distinguished by relatively stronger teeth. More importantly, the ventral valve of permianellid brachiopods, corresponding to their dorsal valve, is also bilobated. The septal apparatus, which is well developed in Lyttoniidae, are completely absent in permianellids. Besides, all permianellids possess a distinctive attachment scar. Youngest representatives of the permianellids have a very complicated central platform. Therefore, we consider that permianellids represent an independent family in the Superfamily Lyttonioidea Waagen.

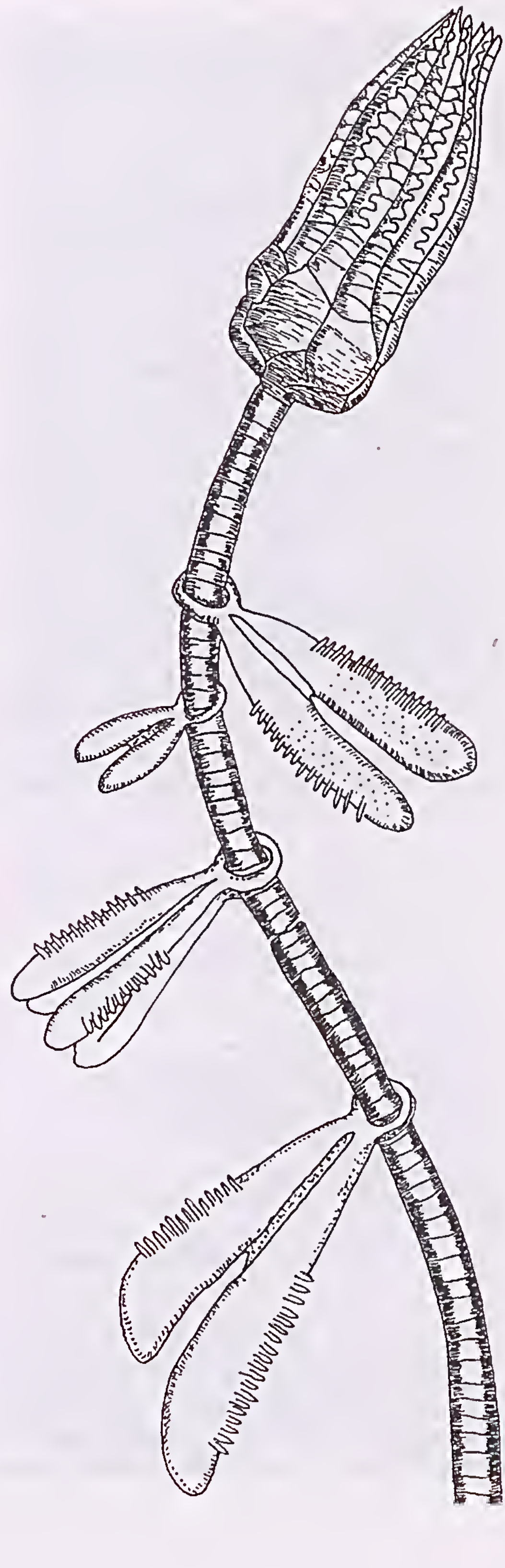

Fig. 4. Living style of permianellids.

Nevertheless, the validity of Permianellidae He & Zhu is still challenged by the subfamily Loczyellinae proposed by Licharew (1937). The genus *Loczyella* was proposed by Frech (1901) with the type species *Loczyella nankingensis* Frech (Frech 1901: 503, pl. 567, fig. 15a–f) from the Chihsia Formation, Nanjing, Jiangsu of China. However, *Loczyella nankingensis* was defined based on a single incomplete and slightly crushed specimen. This specimen does look like some lyttoniids and, possibly, is a permianellid in terms of its external character such as concavo-convex profile, elongate outline and dense concentric lines and no spines on the surface (see Wang et al. 1964: 228, pl. 35, figs 5, 6, 8–11). Licharew (1930) described several specimens from the Upper Permian of North Caucasus as *Loczyella*? *parvula* Licharew, and then (Licharew 1937: 132) proposed the subfamily Loczyellinae and considered that Loczyellinae is much more allied to the Productidae than to the Lyttoniidae. The specimens of *Loczyella*? *parvula* from Caucasus are permianellids (Jin Yugan, pers. comm.). Recently, a similar specimen from Transcaucasia has been named as *Permianella grunti* Shen & Shi (1997: 22, pl. 1, figs 1–7). However, it is still unknown whether the single specimen of *Loczyella nankingensis* Frech is a permianellid or not. If *Loczyella nankingensis* Frech is a permianellid, then the family Permianellidae He & Zhu becomes a junior synonym of Loczyellinae Licharew.

Genus **Dicystoconcha** Termier et al., 1974

Dicystoconcha Termier et al. 1974: 122.—Wang & Jin 1991: 495.
Guangjiayanella Yang 1984: 212.
Guangdongina Mou & Liu 1989: 459.
Dipunctella Liang 1982: 228; 1990: 371.
Obliqunsteges Liang 1990: 373.
Tenerella Liang 1990: 374.
Paristeges Liang 1990: 376-378.
Fabulasteges Liang 1990: 381.
Sicyusella Liang 1990: 383.

Type species. Dicystoconcha lapparenti Termier et al., 1974.

Diagnosis. Shell small to medium in size, elongate bilobate or ovate in outline, concavo- or plano-convex; with sulcus, fold, incision and attachment ring; anterior incision shallow, depth less than half of shell length; marginal brim not developed along the lateral sides of ventral valve. Ventral interior with teeth and central platform; two septa developed on central platform. Dorsal interior with cardinal processes and long brachial ridges. Shell pseudopunctate.

Remarks. The internal details of the type specimen of *Dicystoconcha* from central Afghanistan figured by Termier et al. (1974) are still unknown. Therefore, the distinction between *Dicystoconcha* and other permianellid genera is actually unclear. Similar specimens from Inner Mongolia, China, which were studied by Wang & Jin (1991), show that *Dicystoconcha* probably differs from *Permianella* and *Laterispina* in its absence of any marginal brim along the lateral commissure, relatively shallow anterior incision and two septa on the central platform.

Distribution. Kungurian and Guadalupian; Afghanistan, South China, Northeast China and Southern Primorye of Russia.

Species assigned

Dicystoconcha lapparenti Termier et al. 1974: 123, pl. 22, figs 1, 2; Wang & Jin 1991: 495, pl. 1, figs 1–9; pl. 3, figs 1–7.

Synonyms

Guangjiayanella guangjiayanensis Yang 1984: 212, pl. 31, figs 12–16.
Guangdongina xiaomaoensis Mou & Liu 1989: 458, pl. 1, figs 1–9; pl. 2, figs 1–7; text-fig. 5.
Guangdongina perforans Mou & Liu 1989: 459, pl. 2, fig. 8; pl. 3, figs 1–3.
Guangdongina leguminiformis Mou & Liu 1989: 458, pl. 3, figs 4–8.
Guangdongina sp. Mou & Liu 1989: 459, pl. 2, fig. 9.
Loczyella? *parvula* Likharew & Kotljar 1978: pl. 21, figs 3–4.
Dipunctella stenosulcata Liang 1982: 228, pl. 100, figs 8–9.
Obliqunsteges distortus Liang 1990: 373, pl. 42, fig. 12; pl. 43, fig. 9.
Tenerella usualisa Liang 1990: 374, pl. 42, figs 5–8; pl. 43, figs 1–4, 10–13; text-fig. 49.
Paristeges contracta Liang 1990: 378, pl. 43, figs 7–8.
Paritisteges equilateialis Liang 1990: 379, pl. 42, figs 16–17.
Paritisteges latesulcata Liang 1990: 380, pl. 42, figs 1–2.
Fabulasteges planata Liang 1990: 381, pl. 42, figs 3–4.
Sicyusella regularisa Liang 1990: 383, pl. 43, figs 5–6.

Genus **Litocothia** Grant, 1976

Litocothia Grant 1976: 166.

Type species. Litocothia cateora Grant 1976.

Diagnosis. Shell small; transversely triangular in outline; bilobate with a deep median sulcus; forming a shallow incision at the middle part of the anterior commissure; beak area with a circular attachment ring. Surface smooth except dense growth lines, internal surface entirely smooth. Ventral interior with a high ridge caused by the deep sulcus, but without septum. Dorsal valve unknown.

Comparison. *Litocothia* differs from other genera of the Permianellidae in its smaller size, median ridge inside the ventral valve, and a shallow incision.

Distribution. Wordian (Guadalupian); Ko Muk, Thailand.

Species assigned

Litocothia cateora Grant 1976: 166, pl. 30, figs 19–23.

Genus **Permianella** He & Zhu, 1979

Permianella He & Zhu 1979: 132, 137.—Wang & Jin 1991: 495–496.

Type species. *Permianella typica* He & Zhu 1979.

Diagnosis. Shell medium to large, elongate bilobate in outline, concavo-convex or plano-convex; with sulcus, fold and incision; anterior incision very deep, attaining more than half shell length; irregular marginal brim well developed along the lateral sides of the ventral valve. Ventral interior with teeth and central platform; median septum developed on central platform. Dorsal interior with cardinal process and long brachial ridges. Shell pseudopunctate.

Distribution. Guadalupian to Changhsingian; South China, Thailand, Northeast Japan and Transcaucasia.

Species assigned

Permianella typica He & Zhu 1979: 132, 137, pl. 1, fig. 1a, b; pl. 2, figs 1–3; pl. 3, figs 1–3.—Wang & Jin 1991: 496, pl. 2, figs 1–3.
Permianella grunti Shen & Shi 1997: 22, pl. 1, figs 1–7.
?'*Loczyella*'? *parvula* Licharew 1930: 436, text-figs 1–2; 1937: 83, pl. 13, figs 25–27; Sarytcheva et al., 1960: 238, pl. 42, fig. 5a, b.

Synonyms

Permianella sp. He & Zhu 1979: 133, 139, pl. 1, figs 2–3.
Permianella sp. Tazawa 1987: figs 19–20.
Dipunctella contracta Liang 1982: 229, pl. 102, fig. 3.
Permianella sp. Yanagida et al. 1988, pl. 27, figs 11–13.

Genus **Laterispina** Wang & Jin, 1991

Laterispina Wang & Jin 1991: 496-497.

Type species. *Laterispina liaoi* Wang & Jin, 1991.

Diagnosis. Shell generally large in size, outline bilobate, triangular or belt-shaped; with sulcus in ventral valve; incision very deep; lateral commissure with fence-shaped marginal brim. Ventral interior with a complicated central platform and median septum; internal septa within hollow central platform well developed. Dorsal interior with brachial processes and long longitudinal brachial ridges. Shell pseudopunctate.

Comparisons. *Laterispina* differs from *Permianella* and *Dicystoconcha* in having a complicated fence-shaped margin along lateral side. The margin of *Permianella* is usually irregular and wing-shaped. *Dicystoconcha* lacks margin and a very shallow incision.

Distribution. Guadalupian to Changhsingian; South China and northeast Japan.

Species assigned

Laterispina liaoi Wang & Jin 1991: 497, pl. 2, figs 4–12.
Laterispina parallela Shen et al. 1994: 478; pl. 1, figs 1–12; pl. 2, figs 1–11, 14; text-figs 1–5.

CHRONOSTRATIGRAPHY AND PALAEOBIOGEOGRAPHY OF PERMIANELLIDS

As listed above, a large number of permianellid species have been reported by different authors under various names, herein we group them into four genera including *Dicystoconcha* Termier et al. 1974; *Permianella* He & Zhu 1979; *Litocothia* Grant 1976 and *Laterispina* Wang & Jin 1991. From the tabulated data above, the earliest occurrence of permianellids is probably *Dicystoconcha* Termier et al. from the top part of the Maan Member of the Chihsia Formation in South China. *Litocothia* possesses a very small size and a short triangular outline, however, its hinge line and bilobate outline clearly indicates a close affinity with the genus *Permianella* He & Zhu. The age of the Rat Buri Limestone yielding *Litocothia* is under great dispute. Grant (1976) considered it to be late Artinskian based on his brachiopod analysis. A few fusulinaceans were identified by Sakagami (1969) as *Neofusulinella* and *Ozawainella* and a few bryozoans described by Sakagami (1970) from the same locality were also considered to be of late Artinskian. However, Waterhouse in Waterhouse et al. (1981) analysed the Rat Buri brachiopod ranges and argued for a Kungurian age. The Amb fauna matched with the Rat Buri faunas by Grant (1976) is now redated to be Wordian in terms of conodonts (Wardlaw & Pogue 1995). Another brachiopod fauna similar to the Rat Buri fauna and the Amb brachiopod fauna of the Salt Range is the Khuff brachiopod fauna from the Huqf area on the southern margin of the Arabian Peninsula. The Khuff fauna is clearly of Middle Guadalupian [Wordian (Murgabian)] age based on conodonts and bivalves (Angiolini et al. 1996).

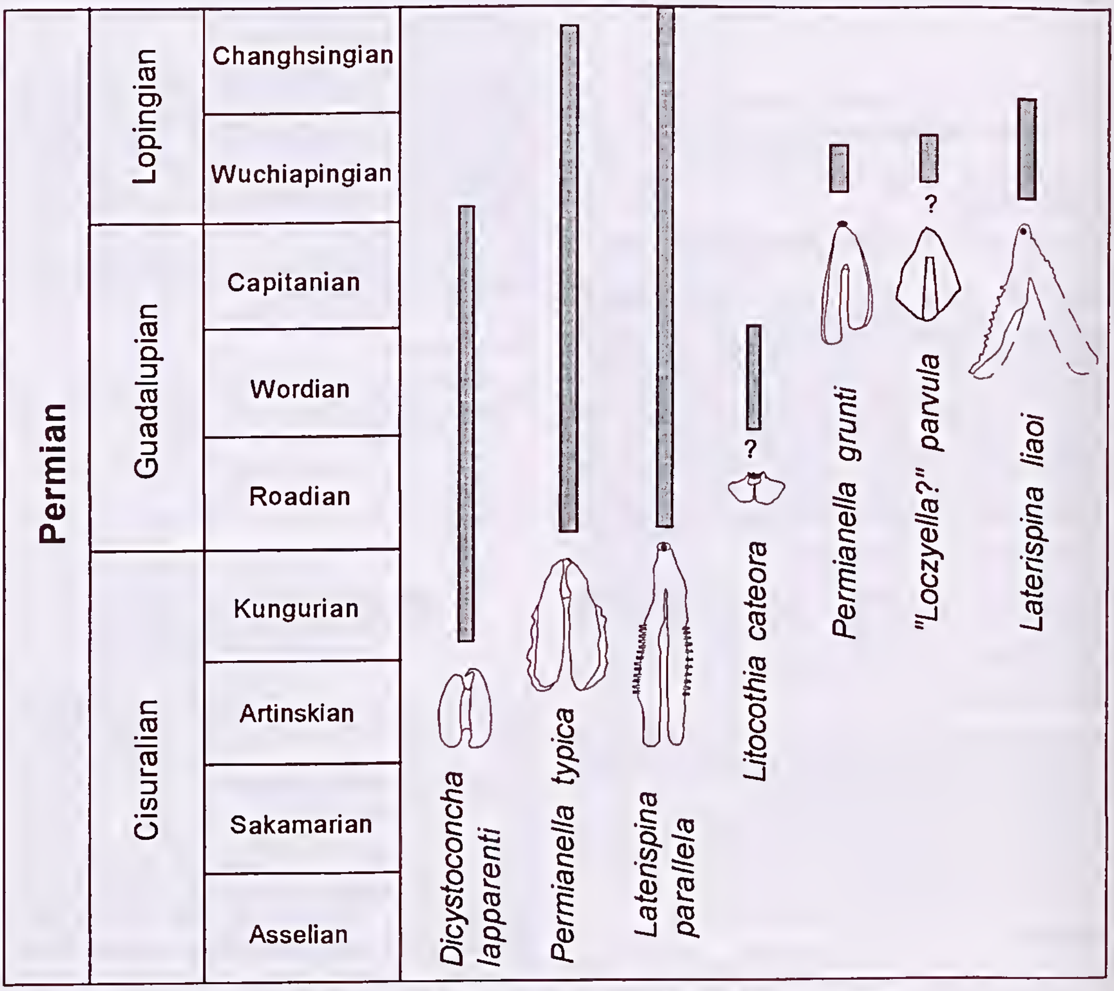

Fig. 5. Stratigraphical range of species in Permianellidae. (Time scale after Jin et al. 1997.)

During the late Guadalupian and Lopingian permianellids became abundant. The uppermost horizon of permianellids is about several centimetres below the Permian–Triassic boundary (Shen et al. 1994) (Fig. 5). Although all permianellids have a bilobate outline and pseudopunctate shell structure, the shape and outline evidently changed with time. The permianellids of the Kungurian and the Wordian are usually small, possess a shallow incision at the middle of the anterior margin and lack a marginal brim along the lateral commissure, as represented by *Dicystoconcha* and *Litocothia*. Permianellids of the Lopingian, such as *Permianella* and *Laterispina*, largely have a relatively long outline, deep incision, and complicated marginal brim. The internal structure of permianellids has received little study because of lack of suitable material or poor preservation. Nevertheless, the central platform normally becomes complicated as revealed by the serial sections made by Shen et al. (1994).

Localities yielding permianellids in the world are shown in Fig. 6. Permianellids are found in limestone, mudstone and siliceous rocks which suggest their wide adaptation to different environments, but they are restricted geographically. Permianellids were mainly confined to the Cathaysian Province of the Eastern Tethys, the mixed zones between the Boreal and Palaeotethyan Realms, and between the Tethyan and Gondwanan Realms (Fig. 7).

Permianellids coexist in the lower part (Kubergandian) of the Kanokura Formation of the Kitakami Mountain of northeast Japan with the fusulinids *Monodiexodina matsubaishi* and *Chusenella chosiensis*, and the brachiopod *Transennatia gratiosus*, *Stenoscisma humbletonensis*, *Mesolobus sinuosa*, *Urushtenoidea maceus*, *Waagenoconcha imperfecta*, *Spiriferellina cristata* and *Martinia* sp. (Tazawa 1987). Recently, Tazawa (1991, 1992) stated that *Permianella* is associated with the Tethyan-type genera *Leptodus*, *Spino-*

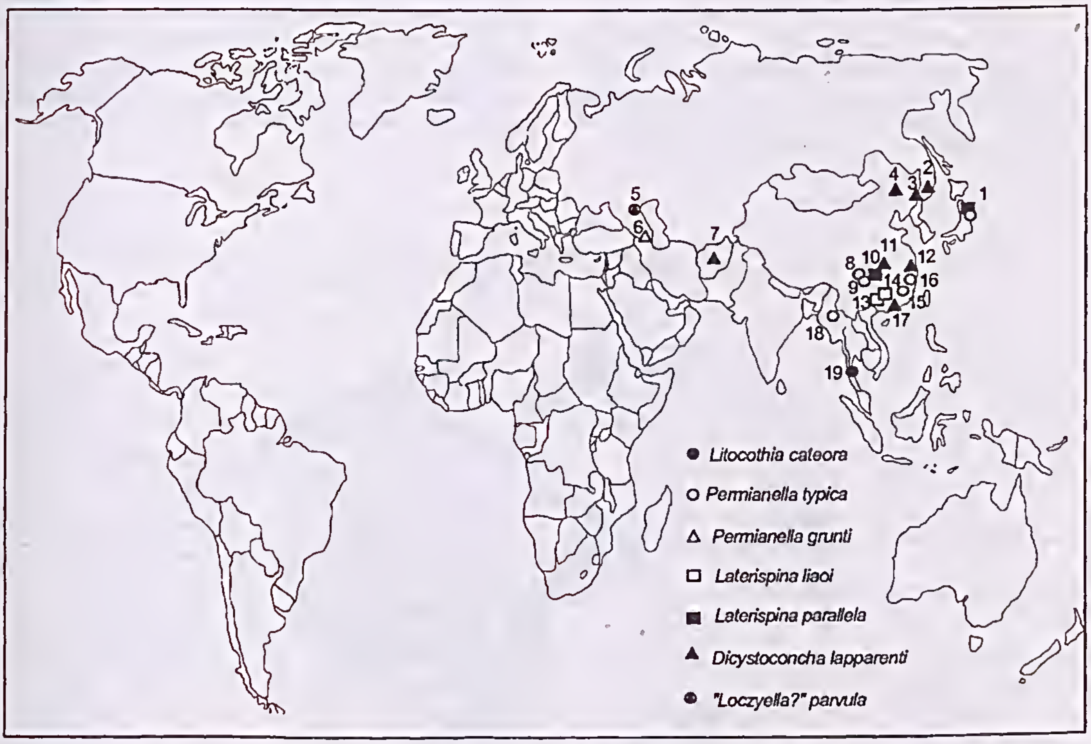

Fig. 6. Map showing the palaeogeographical distribution of Permianellidae. 1. Kitakami Mountains, Japan; 2. Primorye, Russia; 3. Yanbian, Jinlin, China; 4. Zalute Qi, Inner Mongolia, China; 5. North Caucasus, Russia; 6. Dorasham, Nakhichevan; 7. Central Afghanistan; 8. Huayinshan, Sichuan, China; 9. Chongqing, Sichuan, China; 10. Nantong, Sichuan, China; 11. Zigui, Hubei, China; 12. Lengwu Zhejiang, China; 13. Fusui, Guangxi, China; 14. Laibin, Guangxi, China; 15. Jiahe, Hunan, China; 16. Yichun, Jiangxi, China; 17. Guangzhou, Guangdong, China; 18. Tha Wang Pha, Thailand; 19. Ko Muk, Thailand.

marginifera, *Richthofenia*, *Meekella*, *Rhipidomella*, *Geyerella*, *Edriosteges*, *Transennatia*, *Orthothetina*, *Tyloplecta*, *Permundaria*, *Urushtenoidea* and *Cryptospirifer*, as well as with Boreal-type or bipolar genera *Yakovlevia*, *Cancrinella*, *Waagenoconcha*, *Spiriferella* and *Neospirifer*. Besides, the lower part of the Kanokura Formation also contains the brachiopods *Orbiculoidea*, *Isogramma*, *Streptorhynchus*, *Kiangsiella*, *Schuchertella*, *Orthotetes*, *Waagenites*, *Mesolobus*, *Chonetes*, *Wytkina*, *Costiferina*, *Echinoconchus*, *Nantanella*, *Hustedia*, *Uncinulus*, *Spiriferellina*, *Punctospirifer*, *Callispirina*, *Phricodothyris*, *Martinia* and *Whitspakia*. The above-mentioned brachiopod elements show that this fauna is a mixed one between the Cathaysian Province and the Boreal Realm, as already discussed by Tazawa (1991, 1992), Shi et al. (1995) and Shi & Zhan (1996).

It is noticeable that permianellids (*Dicystoconcha*) were also found in the Kedao Formation in the Yanbian district of Jilin and the Liutiaogou Formation in Zalute Qi of Inner Mongolia. In the Kedao Formation the Tethyan-type fusulinids *Neoschwagerina*, *Schubertella*, *Yabeina* and *Verbeekina* were reported, suggesting a correlation with the Kuhfengian of South China (Bureau of Geology and Mineral Resources of Jilin Province 1988). However, the fauna from the lower part of the Kedao Formation in the Kaishantan and Yanji districts contains *Schuchertella*, *Geyerella*, *Plicochonetes*, *Waagenites*, *Hemichonetes*, *Aulosteges*, *Marginifera*, *Spinomarginifera*, *Waagenoconcha*, *Dictyoclostus*, *Permundaria*, *Yakovlevia*, *Leptodus*, *Stenoscisma*, *Neospirifer* and *Spiriferella*, which indicate the mixed character between the Cathaysian and Boreal faunas (Tazawa 1991, 1992; Shi & Zhan 1996).

In Zalute Qi of Inner Mongolia, the genus *Dicystoconcha* is found in the Liutiaogou Formation which mainly consists of grey or dark grey limestone and siltstone containing abundant fusulinids, corals and brachiopods. The main elements include: fusulinids *Parafusulina gruperaensis*, *Skinnerina* sp., *Codonofusiella laxa*, *Reichelina*? sp.; corals *Liangshanophyllum sinense*, *Wentzelella* sp., *Waagenophyllum indicum*, *Calophyllum* sp.; and brachiopods *Enteletes* cf. *andrewsi*, *Derbyella* sp., *Cryptospirifer* sp., *Hustedia grandicosta*, *H. exilis*, *Streptorhynchus* cf. *pelargonatus*, *Waagenites deplanta*, *Spinomarginifera jisuensis*, *Urushtenia* aff. *crenulata*, *Spiriferella* sp., *Stenoscisma purdoni*, *Neospirifer moosakhailensis*, *Richthofenia*? sp., *Haydenella* sp. and *Uncinunellina* sp. According to this list, almost all fusulinids, corals and most brachiopods are Tethyan-type elements. However, the brachiopod *Spiriferella* and *Neospirifer* suggest significant links with those of the Boreal Realm.

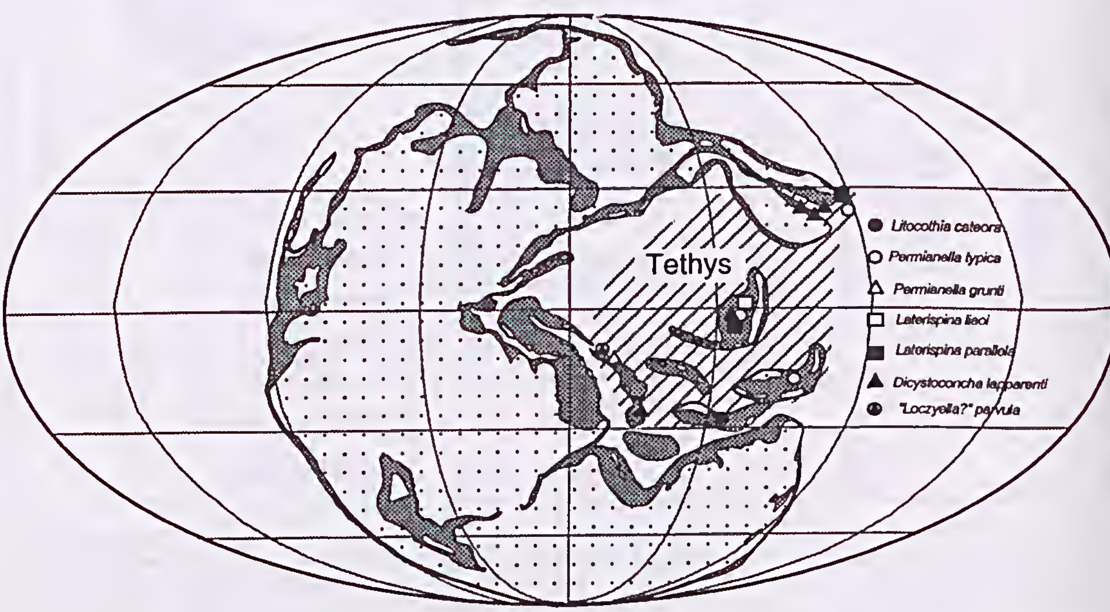

Fig. 7. Distribution of Permianellidae (shadow area) in the Tethys. (Base map after Ziegler et al. 1997; Kazanian.)

Likharew & Kotljar (1978) reported two specimens under the name *Loczyella*? *parvula* Likharew (pl. 21, figs 3–4) from the late Guadalupian *Metadoliolina lepida* Zone in Primorye, Russia. These specimens resemble very closely *Dicystoconcha* in outline. Other common brachiopod representatives in the same zone include *Orthotichia magifica*, *Tyloplecta yangtzeensis*, *Transennatia gratiosus*, *Haydenella tumida* (very similar to *H. kiangsiensis*), *Echinauris opuntia*, *Cancrinella* sp., *Compressoproductus compressus*, *Spinomarginifera jisuensis*, *Marginifera typica*, *Edriosteges poyangensis*, *Leptodus richthofeni*, *Richthofenia orientalis*, *Spirifer reedi*, *S. wynnei*, *Squamularia grandis* etc., most of which are common elements in the Permian of the Cathaysian Province.

A permianellid specimen, *Permianella grunti* Shen & Shi, was also found in the Djhulfian *Araxoceras* Bed in Dorasham of Transcaucasia (Shen & Shi 1997). It is associated with the brachiopods *Acosarina minuta*, *A. dorashamensis*, *Orthothetina dzhulfensis*, *O. peregrina*, *Spinomarginifera spinocostata*, *Compressoproductus djulfensis*, *Haydenella kiangsiensis*, *Leptodus richthofeni*, *Oldhamina transcaucasia*, *Araxathyris protea* and *Permophricodothyris ovata*; the nautiloid *Lopingoceras lopingense*; and the ammonoids *Pseudogastrioceras abichiancum* and *Araxoceras latum*. The associated brachiopod fauna shows that it is undoubtedly typical Tethyan-type (Ruzhentsev & Sarytcheva 1965; Kotljar et al. 1983). Similar specimens from the Upper Permian of North Caucasus were previously described by Licharew (1930, 1937), but their generic states are still unknown.

Permianellids have been reported from 11 localities of South China in the Cathaysian Province. They are usually associated with: the fusulinids *Metadolina*, *Schwagerina*, *Parafusulina*, *Palaeofusulina*; the ammonoids *Shouchangoceras*, *Altudoceras*, *Paraceltites*; and the brachiopods *Tyloplecta*, *Cathaysia*, *Urushtenia*, *Haydenella*, *Edriosteges*, *Leptodus*, *Oldhamina* and *Peltichia*.

Yanagida et al. (1988) reported that *Permianella* was associated with *Chonetinella* sp., *Marginifera* sp., Derbyiinae gen. and sp. indet., *Haydenella* ?sp., and some bryozoans, bivalves, ammonoids and small foraminifers in north Tha Wang Pha, north Thailand. The list of brachiopods suggests an affinity with the Cathaysian faunas. Grant (1976) described 54 brachiopod species assigned to 51 genera from 10 separate limestone hills of southern Thailand. This diverse fauna, containing *Litocothia cateora* Grant, has been interpreted as a manifestation of the much broader mid-Permian transitional biogeographical belt between the warm-water Cathaysian Province and the cold- to temperate Gondwanan Realm (Shi & Archbold 1995; Shi et al. 1995).

Based on the faunal analysis and palaeogeographical distribution mentioned above, it can be concluded that permianellids are largely restricted in the Cathaysian Province but can reach the transitional zones between the Cathaysian and Boreal faunas, and between the Cathaysian and Gondwanan Provinces spanning 30°S and 30°N (Fig. 7) according to the palaeogeographical map of Ziegler et al. (1997).

ACKNOWLEDGEMENTS

This paper is supported by the Australian Research Council (ARC Project A39701265), Deakin University and the Coal Science foundation of the Coal Ministry, People's Republic of China (94 Di10105).

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